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David Ferrier (1843–1928) was born on 13 January 1843 in Woodside, Aberdeen, Scotland, the sixth child of Hannah and David Ferrier. He attended Aberdeen Grammar School and in 1859 he began to study at Aberdeen University, graduating MA with first class honors in classics and philosophy in 1863. As a student, he worked with the psychologist and philosopher Alexander Bain [8, 9]. Following Bain's advice, in 1864 Ferrier went to Germany and joined Helmholtz and Wundt's laboratories to investigate sensory psychophysiology [9]. Back in Scotland, in 1865 he started to study medicine, thereafter graduating MB in 1868 at Edinburgh University. Between 1868 and 1870 he was assistant to the general practitioner William Edmund Image in Bury St Edmunds, Suffolk [7]. Ferrier worked on the corpora quadrigemina and the comparative anatomy of the superior and inferior colliculi, and his MD thesis was awarded a gold medal [7, 10]. In 1870 he moved to London and was appointed as lecturer in physiology at the Middlesex Hospital [4, 8], and in 1871 became neuropathologist at King's College Hospital and worked at the National Hospital for the Paralysed and Epileptic, Queen Square. The following year he succeeded to the chair of forensic medicine [4, 8] and met John Hughlings Jackson, who would have a fundamental mentoring influence on him throughout his entire career [5].

Ferrier and Hughlings Jackson often joined neurological meetings organized by James Crichton-Browne, one of Ferrier classmates in Edinburgh, at the West Riding Lunatic Asylum, mostly discussing the experiments conducted by Gustav Fritsch and Eduard Hitzig by electrically stimulating the brain [7]. In 1873 Crichton-Browne invited Ferrier to work at West Riding Asylum to further investigate this challenging topic [4, 10]. Ferrier had thus the opportunity to stimulate and lesion the brains of birds, cats, dogs, guinea-pigs and rabbits [7]: he was fascinated to

confirm Hughlings Jackson's idea that motor and sensory functions were represented within the cerebral cortex in an organized pattern, through the observation of their behavioral outcomes [3, 5]. Ferrier's first papers on motor cortex were published in his own Institute's house journal, *The West Riding Lunatic Asylum Medical Reports*, and in his *Experimental researches in cerebral physiology and pathology* in 1873 [2, 5, 7].

He discovered that several seizures could be induced in the different types of animals tested, but he also noticed that the overall cerebral organization was nearly the same in different species, even though some parts of the body were more extensively represented in some species [5, 7]. He argued that the seizures he could reproduce in his animals were similar to those observed by Hughlings Jackson in his patients [5, 10]. He also hypothesized that the differences could depend on the habits of the animals, thereby suggesting the existence of a direct relationship between the brain organization and the behavioral specializations in the species [5]. Ferrier employed faradic stimulation, an alternating current applied for intervals longer than the stimulating ones used by Fritsch and Hitzig who, in turn, mainly used galvanic stimulation [6, 7, 9]. In addition, Ferrier focused on greater cortical areas compared to those analyzed by Fritsch and Hitzig, comprehending even the cerebellum [5]. Such methodological discrepancies played a crucial role when Ferrier submitted his work to the *Philosophical Transactions of the Royal Society*. Even if the paper overtly acknowledged the influence of Hughlings Jackson, and Ferrier clearly mentioned his findings as confirmations and further extension of the existing works, the referees criticized him for not giving adequate credit to Fritsch and Hitzig's prior investigations [5].

In 1873, Ferrier returned to King's College London, and at the Brown Animal Sanatory Institute investigated macaques' brains by means of electrical stimulation and ablation [7]. Among others, he identified several centers related to different movements, such as walking, arm retraction, flexion and extension of the wrist, mouth opening, protrusion of the tongue, sneering expressions of the face, and eye movements [5, 7]. In 1874 he became assistant physician both at King's College Hospital and at the West London Hospital. Two years later, he published his pivotal book *The Functions of the Brain* [10]. The cerebral drawings were made by the landscape painter Ernest A. Waterlow: he was the brother of Constance Waterlow, the woman Ferrier married in the very same year, and with whom he later had a daughter and son [7].

In 1878 Ferrier published *The Localizations of Cerebral Disease* as a sort of clinical guide to spatially localize the effects of brain lesions [7]. Following Paul Broca's initial suggestion, Ferrier thus established that sensory–motor functions should be located within cerebral cortex [5, 9]. He was also among the first to transpose monkey cortical

maps to the human brain and to achieve an overall functional neurological mapping for diagnostic purposes. However, given the limits of the available techniques and that his stimulations were not so fine, Ferrier had probably mistaken the visual regions with the angular gyrus [3, 4, 6]. During his career, Ferrier had to cope with antivivisectionist societies, but he could finally demonstrate his innocence throughout his own fundamental discoveries [5].

Ferrier delivered the Croonian lectures twice (in 1874 and 1875), and was elected Fellow of the Royal Society (1876) and of the Royal College of Physicians (1877). Physician in charge of outpatients at King's College Hospital (1881), then Professor of neuropathology (1889) and full physician (1890), in 1908 he was elected Emeritus Professor in the same University. He was notably awarded the Baly Gold Medal, the Royal Medal of the Royal Society and the Cameron Prize of Edinburgh University. Among the founders and editors of the journal *Brain*, he established the Physiological Society, delivered the Harveian Oration and the Goulstonian lecture, contributed to founding the National Society for the Employment of Epileptics, founded and presided over the Neurological Society and the Medical Society of London. Knighted in 1911, during his last years he withdrew from public life. However, he still fulfilled his scientific interests and enjoyed playing golf until an increasing disability stopped him [1]. Ferrier died of pneumonia in London on 19 March 1928. His name is nowadays also attached to the Ferrier lectures delivered every three years in his honor at the Royal Society.

Conflicts of interest The corresponding author states that there is no conflict of interest.

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